

Forest composition following overstory mortality from southern pine beetle and associated treatments¹

T.W. Coleman, Stephen R. Clarke, James R. Meeker, and L.K. Rieske

Abstract: Bark beetle caused mortality continues to play a critical role in determining the composition and structure of forests in North America, and revegetation dynamics following these disturbances are poorly understood. We assessed forest composition following southern pine beetle, *Dendroctonus frontalis* Zimmermann, mortality and associated cut and leave suppression, and compared them with undisturbed loblolly pine, *Pinus taeda* L., stands in Texas. Abundant hardwood regeneration dominated the understory, with little loblolly pine regeneration following either mortality event. Disturbances eliminated loblolly pine dominance in these even-aged stands, thus stratifying forest structure and apparently increasing stem density (stems·ha⁻¹), richness (species·ha⁻¹), and diversity (ha) in the lower strata. Aspect and elevation, presumably through influences on site moisture, were the primary gradients associated with vegetation variation in the canonical correspondence analyses for new regeneration. Mortality from *Dendroctonus* and cut and leave practices shifted loblolly pine communities to mixed upland hardwoods in model predictions generated by the southern variant of the Forest Vegetation Simulator. In addition to being an effective bark beetle control, cut and leave suppression did not alter predicted forest composition 50 years hence when compared with unsuppressed bark beetle-caused mortality. Because of the predicted shift to hardwood domination and a low pine basal area, it is expected that mortality from *D. frontalis* and cut and leave will substantially reduce future hazards from *D. frontalis* outbreaks.

Résumé : La mortalité causée par les scolytes continue d'avoir un impact significatif sur la composition et la structure des forêts en Amérique du Nord et la dynamique de la végétalisation à la suite de ces perturbations est mal comprise. Nous avons évalué la composition de la forêt à la suite de la mortalité causée par le dendroctone méridional du pin (*Dendroctonus frontalis* Zimmermann) et de sa suppression par la méthode qui consiste à couper et à abandonner les débris sur place et nous l'avons comparée à celle de peuplements non perturbés de pin à encens (*Pinus taeda* L.) au Texas. Une régénération abondante de feuillus dominait le sous-étage et la régénération de pin à encens était faible à la suite de l'un ou l'autre des épisodes de mortalité. Les perturbations ont éliminé la dominance du pin à encens dans ces peuplements équiennes, ce qui a entraîné la stratification de la structure de la forêt et l'augmentation apparente de la densité (tiges·ha⁻¹), de la richesse (espèces·ha⁻¹) et de la diversité (ha) en espèces dans les strates inférieures. L'exposition et l'altitude, vraisemblablement à cause de leur influence sur l'humidité de la station, étaient les principaux gradients associés à la variation de la végétation dans les analyses canoniques des correspondances de la régénération récente. La mortalité causée par le dendroctone et les interventions avec la méthode de la coupe et abandon ont transformé les communautés de pin à encens en forêts feuillues mélangées des hautes terres dans les prédictions générées par la variante méridionale du modèle de simulation de la végétation forestière. En plus d'être un moyen de lutte efficace contre les scolytes, la suppression avec la méthode de la coupe et abandon n'a pas modifié la composition prédite de la forêt, même après 50 ans, comparativement à l'absence de suppression de la mortalité causée par les scolytes. Étant donné l'évolution prévue vers une dominance des feuillus et une faible surface terrière du pin, la mortalité causée par le dendroctone ainsi que l'utilisation de la méthode de la coupe et abandon devraient réduire de façon substantielle les risques futurs d'épidémie du dendroctone.

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Introduction

Anthropogenic forces, including altered fire regimes, agriculture and its subsequent abandonment, timber production,

and forest management, altered pre-European forests of the southeastern United States, transforming prevalent open, park-like savannahs of longleaf pine (*Pinus palustris* Mill.) into dense, even-aged forests of loblolly pine (*Pinus taeda*

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L.; Landers et al. 1995). These changes in forest composition have led to substantial increases in populations of southern pine beetle (*Dendroctonus frontalis* Zimmermann), forest susceptibility to attack by this insect, and hence, outbreak susceptibility (Clarke and Billings 2003).

Dendroctonus frontalis is the most significant indigenous biotic threat to southeastern forests (Schowalter et al. 1981). *Dendroctonus frontalis* feeds en masse on the phloem of pine, typically those greater than poletimber size (≥ 12.7 cm diameter at breast height, DBH), essentially girdling the tree and leading to tree mortality (Payne 1980). Favored hosts are loblolly and shortleaf pines (*Pinus echinata* Mill.), but it is capable of utilizing more than 18 *Pinus* species (Payne 1980).

Dendroctonus frontalis outbreaks can occur every 6–12 years in southern portions of its range, and persist for 2–3 years (Turchin et al. 1999). Over the past several decades, the time between outbreaks has decreased, whereas the scale and intensity of these outbreaks has increased (Price et al. 1992). During outbreak years, the entire pine overstory may be killed, thus causing tremendous economic losses, altering nutrient cycling and watershed characteristics, and impacting pine-dependent wildlife and plant communities (Leuschner 1980).

The USDA Forest Service routinely suppresses all expanding and threatening *D. frontalis* infestations on public lands, with the exception of those outbreaks occurring in areas designated as “wilderness.” Two suppression tactics, cut and leave (C–L) and cut and remove, are implemented to suppress *D. frontalis* infestations, prevent large-scale pine mortality, and reduce timber losses (Billings 1980; Clarke and Billings 2003). Both tactics are directed at cutting all infested pines containing living beetle as well as a buffer strip of susceptible pines in front of beetle activity to stop further expansion of the infestation.

In the C–L approach, felled pine trees are left in the forest because of management restrictions, inaccessibility for timber removal, or poor market conditions. Although C–L avoids the additional disturbances of timber harvesting practices, such as log skidding and soil compaction, it is not as effective for suppressing larger outbreaks or during cooler temperatures when beetle populations within felled trees are not exposed to lethal summer temperatures. Cut and remove is similar to C–L, except the cut timber is salvaged and removed from the forest. Cut and remove suppression removes *D. frontalis* populations from the forest with the felled timber, diminishing the likelihood of outbreak expansion and potentially generating revenue from the timber resource.

Pine mortality from both *D. frontalis* and associated suppression practices can result in widespread forest canopy loss and extensive changes in light availability, temperature, growing space, soil moisture, and competition (Pacala et al. 1994; Palik et al. 1997; McGuire et al. 2001). Physical disturbances, including mortality events associated with *D. frontalis*, are thought to generate conditions favorable for regeneration of early successional species like pine and vegetation recruitment and growth (Sousa 1984).

Natural vegetation succession following disturbances associated with *D. frontalis* has received little attention, and knowledge of the mechanisms of forest regeneration and the biotic and abiotic factors influencing revegetation dynamics

is limited. Our objective was to assess the influence of widespread forest disturbance following mortality from *D. frontalis* and C–L on vegetation composition, stand structure, and forest succession and to determine if C–L influences forest stand dynamics differently than unsuppressed mortality caused by *D. frontalis*. These two disturbance events were referenced to each other and to nearby undisturbed loblolly pine stands of similar age and composition prior to disturbance on the western Gulf Coastal Plain, United States. Field assessments occurred approximately 12 years after the disturbance events to allow establishment and expression of subsequent forest type(s). In addition, we assessed environmental variables influencing woody plant composition and modeled current vegetation data to predict future forest composition. Modeling future forest composition and stand structure following mortality caused by *D. frontalis* and associated suppression will supply forest managers with stand hazard ratings for *D. frontalis*, which can be used to schedule thinning activities to reduce forest susceptibility.

We predicted that mortality caused by *D. frontalis* and C–L would shift initial pine communities to primarily hardwood composition by enhancing the light availability to the forest floor and alleviating competition from overstory pines. The C–L was expected to have greater pine regeneration than mortality caused by *D. frontalis* alone, because of increased growing space from the immediate removal of the canopy. These disturbances were also predicted to reduce future forest susceptibility to *D. frontalis* outbreaks because of the release of established hardwoods competition, which had previously limited pine regeneration, and sporadic pine regeneration that seeded naturally versus high densities planted for timber production.

Materials and methods

Description of sites

We focused on two wildernesses in the piney woods region of eastern Texas with a history of large-scale *D. frontalis* outbreaks. This region is characterized by an annual mean maximum temperature of 28.1 °C, a minimum mean temperature of 9.3 °C, and annual precipitation of 109 cm (National Weather Service 2001). Each wilderness experienced extensive pine mortality caused by *D. frontalis* and associated C–L.

Indian Mounds Wilderness (Sabine National Forest, Sabine County, Texas) consists of 4466 ha of loblolly pine, loblolly pine – hardwood, and white oak – southern red oak – hickory (*Quercus alba* L. – *Quercus falcata* Michx. – *Carya* spp.) forest types. During 1991 and 1992, *D. frontalis* outbreaks destroyed over 3365 ha (~75%) of loblolly pine forests in Indian Mounds. Ten C–L events, covering several forest stands and comprising an estimated 8 ha, were used to suppress expanding infestations threatening adjacent private land, according to protocols designated for wilderness (USDA Forest Service 1987). No major disturbance events have subsequently impacted the area.

Turkey Hill Wilderness (Angelina National Forest, Angelina County, Texas) encompasses 2139 ha comprising mainly loblolly pine, longleaf pine, and white oak – southern red oak – hickory forest types. In Turkey Hill, *D. frontalis* destroyed pines on 860 ha (~40%) of forests during 1992–

1993 (Clarke and Billings 2003). Nine C–L events, covering ~9 ha across several stands, suppressed actively advancing outbreaks threatening private lands. No major disturbances have occurred since.

Disturbance regimes

We compared current and predicted (50 years hence) vegetation composition in three disturbance regimes: (i) mortality caused by *D. frontalis* (SPB), (ii) C–L, and (iii) undisturbed control pine stands (CON). Fifty forest stands were assessed in the two wildernesses, including SPB ($N = 20$), C–L ($N = 10$), and CON ($N = 20$). Stand treatments were equally divided between the two wildernesses. Because of management restrictions associated with wildernesses, C–L represented <1% of the mortality in each wilderness, thereby limiting the number of available replicates. We focused on forest stands ranging from 10 to 300 ha that were defined and managed as loblolly pine forest type by the USDA Forest Service prior to wilderness designation (USDA Forest Service 1985). In our study, vegetation and forest stand assessments occurred in the wildernesses in 2004 and 2005, approximately 12 years after SPB and C–L.

Sampling design and assessments

In each loblolly pine stand, five 0.04 ha fixed-radius whole plots were established a minimum of 50 m from forest stand edges and separated by a minimum of 50 m to survey woody plant vegetation and assess stand characteristics and landscape variables. Ten subplots, five 0.004 ha and five 0.0004 ha, were nested within each whole plot (0.04 ha) to enhance precision of our vegetation assessments. Whole plots (0.04 ha) were used to assess overstory and midstory vegetation, whereas 0.004 ha subplots were used to assess saplings and shrubs (≥ 137 cm height), and 0.0004 ha subplots were used to assess seedlings, shrubs (<137 cm height), and vines. One of each subplot size was positioned at the whole plot center and in each cardinal direction, 7.7 m from the plot center. Thus, a surveyed stand contained a total of five 0.04 ha whole plots, twenty-five 0.004 ha subplots, and twenty-five 0.0004 ha subplots. Measurements of vegetation and plot data followed the Common Stand Exam protocols of the USDA Forest Service's Natural Resource Information System (NRIS): Field Sampled Vegetation Module (FSVeg) (USDA Forest Service 2003).

In the whole plots (0.04 ha), all living overstory and mid-story trees (≥ 12.7 cm DBH) were assessed by species, diameter at breast height (DBH), height, and crown height (distance to lowest continuous part of the crown).

In the 0.004 ha subplots, all live saplings (≤ 12.7 cm DBH) and shrubs (≥ 137 cm height) were identified and measured following the same protocol as in the whole plots (0.04 ha). Lastly, seedlings, shrubs, and vines (<137 cm height) were identified and plant height assessed in each of the 0.0004 ha subplots.

Aspect, elevation, slope (%), and slope position (summit, shoulder, backslope, footslope, toeslope, and valley bottom) were assessed in each whole plot (0.04 ha) (USDA Forest Service 2003). Tree growth over the previous 10 years was estimated by increment boring two dominant hardwoods of the same species and two dominant pines of the same species, if available in each whole plot (0.04 ha) and measuring

the width of each of the last 10 growth rings to the nearest 0.13 cm. Tree ring data were incorporated into the modeling for growth estimates. The presence and relative abundance of nonnative, invasive woody plants were noted. In addition, forest stand age was assessed for each loblolly pine stand using historic data (USDA Forest Service 1985).

Forest modeling

Forest stand succession, structure, and forest type (SAF 1965; Arner et al. 1998; Donnelly et al. 2001), were modeled 50 years into the future from 2004 or 2005 utilizing the southern variant of the Forest Vegetation Simulator (FVS) (USDA Forest Service 2001). Assessed tree data and landscape variables, including species, DBH, height, height to crown, radial growth, and eastern Texas species growth data, were incorporated into the FVS to calibrate and model forest stand succession on a 5 year cycle (Donnelly et al. 2001). Loblolly pine stand parameters (maximum stand density index and maximum basal area) were used to regulate forest stand modeling. Predicted forest type (>50% canopy composition) and stand characteristics were obtained from FVS by using the main output, and stand and stocking simulators.

The FVS is an individual-tree, nonspatial forest growth model built from the core model Prognosis (Stage 1973). FVS is nationally supported, and Robinson and Monserud (2003) found it to be the most adaptable among several modeling programs, in part because of the availability of regional variants. The FVS is capable of predicting long-term ecosystem changes (Teck et al. 1996) and is adequate for simulating future stand conditions where growth is the dominant process (Sesnie and Bailey 2003). Extensive use and verification of the southern variant of the FVS is currently lacking, mainly because of its recent conception. However, other variants built from the same core as the southern variant have shown accuracy for predicted tree density and diameter, and stand characteristics were accurate to within $\pm 20\%$ of measured data (Fule et al. 2004). The FVS variants tend to underestimate top height and basal area but correctly predict the distribution of diameter size classes (Lacerte et al. 2004). Groot et al. (2004) state that long-term modeling may pose problems for FVS, but our fairly short-term projections (50 years) may not significantly exaggerate stand characteristics. Regardless, modeling results should be used with caution.

Statistical analysis

Woody plant density (stems·ha⁻¹), richness (species·ha⁻¹), diversity (ha), and evenness (ha) were compared among the three disturbance regimes (SPB, C–L, and CON). Diversity was calculated using the Shannon index (H' ; Magurran 1988):

$$[1] \quad H' = -\sum p_i \ln p_i$$

where p_i is the number of plants surveyed in species i divided by the total number of plants per plot. Evenness was calculated using Pielou's evenness index (J' ; Magurran 1988):

$$[2] \quad J' = \frac{H'}{\ln S}$$

where S is species richness. Plant indices were calculated for three size classes: overstory and midstory woody species

(≥ 12.7 cm DBH), saplings (< 12.7 cm DBH) and shrubs (≥ 137 cm height), and seedlings, shrubs (< 137 cm height), and vines. Plant counts for all three size classes were adjusted to a per-hectare basis to standardize counts for all analyses.

Current basal area ($\text{m}^2\cdot\text{ha}^{-1}$) was calculated for two size classes (overstory and midstory; saplings and shrubs) to determine forest susceptibility to *D. frontalis*. Predicted basal area from FVS simulations focused on overstory (> 25.4 cm DBH), midstory (12.7–25.3 cm DBH), and saplings. For the FVS predictions, we assessed basal area for all tree species and, specifically, for loblolly pine.

We used a mixed-model analysis of variance (ANOVA) with a randomized complete block design (PROC MIXED; SAS Institute Inc. 1997) to test for differences in community parameters, basal area, and modeled forest type between the three disturbance regimes. Wilderness (Indian Mounds and Turkey Hill) was designated as the blocking effect, disturbance regime as the fixed effect, and stand as a random effect. Whole plots and subplots were used as subsamples of stands. Tukey's pairwise test was used for assessing multiple comparisons. We transformed data (logarithmic) if it did not meet underlying assumptions of normality and homogeneity of variances (Levene's equal variances test) for analyses of variance. In the results, data are presented as untransformed means \pm SEs to assist with interpretation. For all analyses, treatment effects were considered statistically significant if $P \leq 0.05$; however, consideration was also given to those effects of marginal significance ($P = 0.09$ – 0.05) because of the complexity and variability of the system.

We used multivariate analysis of variance (MANOVA) to assess differences among disturbance regimes and wilderness units in the five most abundant plant species for each size class (PROC GLM; SAS Institute Inc. 1997). Overall significance in the MANOVA was assessed using the Wilks' λ test statistic. The same statistical design, effects, pairwise test, and assumption tests were used for this analysis as in the ANOVA. The five most abundant species were incorporated into the analysis to focus on those species holding dominant positions in each size class and to depict current forest structure; the entire plant community was assessed using ordination.

Direct gradient analysis was used to determine if gradients in woody species composition existed and to assess the influence of environmental variables in determining species distribution (Blake and Schuetz 2000). Canonical correspondence analysis (CCA) was used to examine the relationship among samples in each of the three size classes (ter Braak 1986; PC-ORD, McCune and Mefford 1999). CCA depicts the influence of disturbance regimes on the entire vegetation community, unlike FVS, which only incorporates tree species. Identifying the initial (i.e., 12 years postdisturbance) and undisturbed forest types assists in forest planning, and provides guidance for the type of management action necessary to achieve a desired result.

Relationships among species and stands to the measured environmental variables are presented graphically.

Plant species counts and environmental variables were incorporated into the CCA at the stand level ($N = 50$). Aspect, elevation, slope (%), stand age, and stand treatments (SPB, C–L, and CON) were included as environmental variables in the analyses. Environmental variables describe mean stand conditions; plant density was standardized on a per-hectare basis. Aspect was transformed to a 0–16 scale, from 0 (NNE 40° ; most mesic) to 16 (SSW 220° ; most xeric), modified from Dargie (1984). Plot elevation ranged from about 22 to 114 m. Stand ages spanned from 53 to 99 years, with a mean age of 67 years for each wilderness. The three disturbance regimes were incorporated into the analysis as dummy (one or zero) variables ($K - 1$); as a result, undisturbed plots were not assessed.

The first three ordination axes were used to examine the variation extracted from the data. Eigenvalues are presented to show variance extracted by environmental variables. Intraset correlations coefficients ≥ 0.60 are used to show the relative importance of each environmental variable in the overall community (ter Braak 1986). Axis scores and Pearson's correlation coefficients were used to interpret species associations with each axis.

Forest types predicted by FVS were analyzed using a chi-square (χ^2) analysis with Fisher's exact test. Chi square analysis tested the frequency of predicted forest types, pine-dominated canopies (pine basal area $> 50\%$ of the dominant canopy species) and hardwood-dominated canopies (hardwood basal area $> 50\%$ of the dominant canopy species), across the three treatments and compared pine versus hardwood dominance among the three treatments.

Results

We surveyed 71 853 individual woody plants in 96 species (Appendix A)³. There were 33 435 individuals in the SPB stands, 16 260 in the C–L stands, and 22 158 in CON stands. No non-native, invasive woody plant species were observed. Only statistically significant differences are addressed.

Overstory and midstory

In the overstory and midstory, SPB and C–L had significantly lower plant stem densities relative to CON stands (Table 1). In Indian Mounds, both disturbances associated with SPB had significantly lower overstory and midstory richness and diversity compared with CON stands (Table 1); however, the corresponding differences were nonsignificant at Turkey Hill. Overstory and midstory evenness was more even in C–L stands relative to CON stands in Turkey Hill (Table 1).

The five most abundant overstory and midstory trees included loblolly pine, white oak, sweetgum (*Liquidambar styraciflua* L.), red maple (*Acer rubrum* L.), and southern red oak (Table 2). In Indian Mounds and Turkey Hill, SPB and C–L disturbances each had less loblolly pine density than CON stands (Table 2).

³Supplementary data for this article are available on the journal Web site (cjfr.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 3740. For more information on obtaining material refer to cisti-icist.nrc-cnrc.gc.ca/cms/unpub_e.html.

Table 1. Woody plant community following pine mortality from *Dendroctonus frontalis* and cut and leave suppression in loblolly pine stands.

Parameter and site	ANOVA		Disturbance regime		
	$F_{[2,43]}$	P	<i>D. frontalis</i> (SPB)	Cut and leave (C-L)	Undisturbed (CON)
Overstory and midstory					
Density (stems·ha ⁻¹)	45.1	<0.0001 (D)	261 (9.31)b	236 (14.5)b	414 (12.3)a
Richness (species·ha ⁻¹)	6.55	0.003 (D × W)			
Indian Mounds			4.46 (0.22)b	4.12 (0.41)b	6.36 (0.19)a
Turkey Hill			5.88 (0.22)a	6.28 (0.30)a	6.0 (0.28)a
Diversity (ha)	9.04	0.005 (D × W)			
Indian Mounds			1.29 (0.06)b	1.18 (0.10)b	1.62 (0.03)a
Turkey Hill			1.55 (0.05)a	1.66 (0.06)a	1.47 (0.05)a
Evenness (ha)	3.96	0.03 (D × W)			
Indian Mound			0.884 (0.02)a	0.826 (0.05)a	0.885 (0.01)a
Turkey Hill			0.875 (0.02)a	0.913 (0.02)a	0.841 (0.01)b
Saplings and shrubs (≥137 cm height)					
Density (stems·ha ⁻¹)	6.10	0.005 (D × W)			
Indian Mounds			33 215 (1 719)a	30 490 (2 518)a	15 620 (1 057)b
Turkey Hill			18 415 (1 199)b	33 840 (2 418)a	11 445 (1 029)b
Richness (species·ha ⁻¹)	3.45	0.04 (D × W)			
Indian Mounds			19 (0.55)a	19 (1.09)a	12 (0.62)b
Turkey Hill			15 (0.58)b	19 (0.67)a	11 (0.48)c
Diversity (ha)	18.5	<0.0001 (D)	2.18 (0.04)a	2.34 (0.05)a	1.81 (0.04)b
Evenness (ha)	—	ns	0.788 (0.01)a	0.801 (0.01)a	0.762 (0.01)a
Seedlings, shrubs (<137 cm height), and vines					
Density (stems·ha ⁻¹)	6.70	0.003 (D × W)			
Indian Mounds			474 905 (39 368)a	288 260 (22 889)a	349 130 (34 337)a
Turkey Hill			737 150 (49 390)a	744 330 (67 101)a	320 530 (29 806)b
Richness (species·ha ⁻¹)	3.56	0.04 (D × W)			
Indian Mounds			21 (0.64)a	19 (0.49)b	16 (0.65)b
Turkey Hill			23 (0.41)a	22 (0.57)a	15 (0.48)b
Diversity (ha)	2.58	0.09 (D)	2.17 (0.05)a	2.15 (0.06)b	1.97 (0.05)b
Evenness (ha)	3.30	0.05 (D × W)			
Indian Mounds			0.716 (0.02)a	0.797 (0.02)a	0.697 (0.02)a
Turkey Hill			0.691 (0.02)a	0.640 (0.03)b	0.748 (0.02)a

Note: Values are means with SEs given in parentheses. Values with the same letters in a row are not significantly different. ($P > 0.05$). The values for the individual sites are only given where a significant disturbance by site interaction occurred. ANOVA effects: D, disturbance; D × W, disturbance by wilderness (site) interaction; ns, not significant.

Overstory and midstory basal area was less in SPB and C-L stands relative to CON stands (Table 3). SPB stands had significantly greater basal area relative to C-L stands (Table 3). Fifty years hence, both SPB and C-L are predicted to cause significant reductions in overstory basal area relative to CON stands (Table 3). The FVS model predicts SPB will possess significantly greater midstory basal area relative to C-L and CON stands (Table 3).

Saplings and shrubs (≥137 cm height)

SPB and C-L disturbance had greater sapling and shrub density and richness relative to CON stands at Indian Mounds (Table 1). In Turkey Hill, C-L stands had larger sapling and shrub densities than either SPB or CON stands (Table 1). C-L possessed greater richness over SPB stands, and over CON stands in Turkey Hill. SPB stands also had more sapling and shrub richness and diversity relative to CON stands, whereas C-L had less diversity (Table 1).

The five most abundant sapling- and shrub-sized plants included yaupon (*Ilex vomitoria* Ait.), sweetgum, red maple, American beautyberry (*Callicarpa americana* L.), and hop

hornbeam (*Ostrya virginiana* (Mill.) K. Koch; Table 2). Red maple saplings were significantly greater following SPB and C-L and were more abundant in C-L than SPB stands (Table 2). In Turkey Hill, American beautyberry was greater following SPB and C-L (Table 2) and was more dense in C-L stands than in SPB stands (Table 2). Hop hornbeam saplings were greater following SPB relative to CON stands (Table 2).

In Indian Mounds, basal area of sapling and shrubs was equivalent between SPB and C-L but significantly greater compared with CON stands in FVS predictions (Table 3). In 50 year model projections, sapling basal area predictions were larger in C-L compared with SPB stands and CON stands (Table 3).

Seedlings, shrubs (<137 cm height), and vines

In Turkey Hill, both disturbances had significantly greater seedling, shrub, and vine density and richness relative to CON stands (Table 1). CON stands were more even in the understory compared with C-L stands at Turkey Hill. In Indian Mounds, SPB possessed more species richness rela-

Table 2. The five most abundant woody plant species in three size classes in loblolly pine stands following mortality from *D. frontalis* and cut and leave suppression.

Species	ANOVA			Disturbance regime		
	<i>F</i>	df	<i>P</i>	<i>D. frontalis</i> (SPB)	Cut and leave (C–L)	Undisturbed (CON)
Overstory and midstory (stems·ha⁻¹)						
Wilk's lambda	2.15	10, 80	0.03 (D × W)			
Loblolly pine (<i>Pinus taeda</i>)	8.07	2, 44	0.001 (D × W)			
Indian Mound				15 (3.9)b	16 (7.9)b	77 (7.3)a
Turkey Hill				5.0 (1.9)b	16 (7.3)b	173 (14.4)a
White oak (<i>Quercus alba</i>)	—		ns	55 (5.4)a	37 (6.4)a	37 (4.7)a
Sweetgum (<i>Liquidambar styraciflua</i>)	—		ns	34 (4.3)a	34 (5.2)a	47 (5.0)a
Red maple (<i>Acer rubrum</i>)	—		ns	26 (3.2)a	25 (5.3)a	29 (4.2)a
Southern red oak (<i>Quercus falcata</i>)	—		ns	17 (2.8)a	21 (4.2)a	28 (3.3)a
Saplings and shrubs (≥137 cm height) (stems·ha⁻¹)						
Wilk's lambda	3.02	10, 80	0.003 (D × W)			
Yaupon (<i>Ilex vomitoria</i>)	—		ns	5 175 (612)a	6 275 (1 161)a	4 108 (430)a
Sweetgum (<i>Liquidambar styraciflua</i>)	—		ns	1 850 (222)a	1 750 (291)a	1 965 (270)a
Red maple (<i>Acer rubrum</i>)	7.93	2, 44	0.001 (D × W)	1 660 (195)b	2 745 (267)a	1 003 (129)c
American beautyberry (<i>Callicarpa americana</i>)	9.11	2, 44	0.0005 (D × W)			
Indian Mounds				760 (152)a	390 (102)a	75 (39)a
Turkey Hill				2 610 (467)b	4 890 (791)a	360 (96)c
Hop hornbeam (<i>Ostrya virginiana</i>)	3.78	2, 44	0.03 (D)	1 503 (219)a	1 150 (288)ab	435 (107)b
Seedlings, shrubs (<137 cm height), and vines (stems·ha⁻¹)						
Wilk's lambda	3.60	10, 80	0.0005 (D × W)			
Poison ivy (<i>Toxicodendron radicans</i>)	4.88	2, 44	0.01 (D × W)			
Indian Mounds				129 250 (34 807)a	24 720 (16 981)a	123 775 (32 148)a
Turkey Hill				92 895 (28 154)ab	290 080 (73 789)a	16 950 (3 649)b
Roundleaf greenbrier (<i>Smilax rotundifolia</i>)	—		ns	47 560 (13 188)a	56 270 (14 813)a	27 117 (3 692)a
Sarsaparilla-vine (<i>Smilax pumila</i>)	—		ns	65 078 (18 148)a	6 650 (3 614)a	32 787 (12 520)a
Sweetgum (<i>Liquidambar styraciflua</i>)	6.13	2, 44	0.005 (D × W)			
Indian Mounds				14 450 (4 378)a	3 400 (1 040)a	3 700 (932)a
Turkey Hill				87 350 (12 838)a	49 300 (11 136)ab	7 450 (1 915)b
Evening trumpetflower (<i>Gelsemium sempervirens</i>)	—		ns	35 325 (5 319)a	29 000 (4 863)a	14 225 (1 945)a

Note: Values are means with SEs given in parentheses. Values with the same letters in a row are not significantly different. ($P > 0.05$). The values for the individual sites are only given where a significant disturbance by site interaction occurred. ANOVA effects: D, disturbance; D × W, disturbance by wilderness interaction; ns, not significant.

Table 3. Current and modeled (based on FVS stand simulations, 50 years) basal area and significant differences following mortality from *D. frontalis* and cut and leave suppression in two Texas wildernesses.

Forest story and site	ANOVA		Disturbance regime		
	$F_{[2,43]}$	P	<i>D. frontalis</i> (SPB)	Cut and leave (C–L)	Undisturbed (CON)
Current					
Overstory and midstory (≥ 12.7 cm DBH)	162	<0.0001 (D)	15.8 (0.89)b	11.5 (0.93)c	38.4 (0.95)a
Saplings and shrubs (≥ 137 cm height)	6.48	0.004 (D \times W)			
Indian Mounds			36.7 (3.56)a	37.9 (7.68)a	16.9 (1.39)b
Turkey Hill			16.5 (1.27)a	21.9 (1.62)a	24.7 (5.51)a
Modeled					
Overstory (> 25.4 cm DBH)	9.99	0.0003 (D)	8.64 (1.42)b	10.9 (1.54)b	20.3 (2.52)a
Loblolly pine overstory	—	ns	3.34 (1.07)a	3.14 (1.09)a	7.36 (2.36)a
Midstory (12.7–25.3 cm DBH)	7.24	0.002 (D)	25.8 (1.89)a	17.0 (2.94)b	16.0 (2.11)b
Loblolly pine midstory	—	ns	2.75 (1.27)a	3.55 (0.99)a	6.56 (1.96)a
Sapling (≥ 137 cm height)	3.73	0.03 (D)	9.51 (1.98)b	18.7 (3.75)a	13.8 (1.83)b
Loblolly pine sapling	—	ns	1.16 (1.12)a	0.21 (0.175)a	0.51 (0.27)a

Note: Values are means with SEs given in parentheses. Values with the same letters in a row are not significantly different. ($P > 0.05$). The values for the individual sites are only given where a significant disturbance by site interaction occurred. ANOVA effects: D, disturbance; D \times W, disturbance by wilderness (site) interaction. ns, not significant.

Table 4. Canonical correspondence analysis of species in three size classes and environmental variables following mortality from *Dendroctonus frontalis* and cut and leave suppression.

	Axis		
	1	2	3
Overstory and midstory (36 species)			
Eigenvalues	0.282	0.115	0.040
Species–environment correlations	0.921	0.722	0.670
Cumulative percentage of variance of species data	11.6	16.3	17.9
Intrasect correlation for environmental variables			
Aspect	0.481	–0.397	0.097
Elevation	0.405	–0.528	0.397
Slope	–0.485	0.601	0.503
Stand age	–0.275	0.039	0.392
<i>Dendroctonus frontalis</i> (SPB)	–0.786	–0.201	0.208
Cut and leave (C–L)	–0.308	0.074	–0.331
Saplings and shrubs (≥ 137 cm height) (77 species)			
Eigenvalues	0.199	0.139	0.087
Species–environment correlations	0.817	0.749	0.750
Cumulative percentage of variance of species data	7.8	13.2	16.6
Intrasect correlation for environmental variables			
Aspect	–0.712	–0.119	–0.401
Elevation	–0.721	0.324	0.176
Slope	0.615	0.584	–0.401
Stand age	0.296	0.497	0.706
<i>Dendroctonus frontalis</i> (SPB)	0.252	0.019	–0.524
Cut and leave (C–L)	–0.160	0.321	0.187
Seedlings, shrubs (< 137 cm height), and vines (89 species)			
Eigenvalues	0.230	0.138	0.066
Species–environment correlations	0.757	0.805	0.496
Cumulative percentage of variance of species data	8.9	14.3	16.9
Intrasect correlation for environmental variables			
Aspect	–0.659	–0.613	–0.004
Elevation	–0.661	–0.110	–0.076
Slope	0.440	0.518	–0.263
Stand age	0.153	0.186	0.315
<i>Dendroctonus frontalis</i> (SPB)	–0.086	0.606	0.651
Cut and leave (C–L)	–0.063	0.160	–0.826

Fig. 1. Canonical correspondence analysis for overstory and midstory (a), sapling and shrub (≥ 137 cm height) (b), and seedling, shrub (< 137 cm height), and vine (c and d) size classes following mortality from *Dendroctonus frontalis* and cut and leave suppression, and in undisturbed loblolly pine stands. Solid circles, *D. frontalis* disturbance; solid triangles, cut and leave suppression; open squares, undisturbed pine stands. Only the most abundant species (+) for each size classes are labeled if present. Species abbreviations are the first three letters of the genus and species names (full names are given in Table 2). Correlations among species, stands, and environmental variables are shown as radiating vector lines or the relative location of stand treatments (Asp., aspect; C–L, cut and leave; Elv., elevation; Slp., slope; SPB, *D. frontalis*; Sta., stand age). Figure 1 appears on the following pages.

tive to CON C–L and C–L stands (Table 1). Seedling, shrub, and vine diversity was marginally larger following SPB compared with CON stands ($P = 0.08$, Table 1).

Poison ivy (*Toxicodendron radicans* (L.) Kuntze), round-leaf greenbrier (*Smilax rotundifolia* L.), sarsparilla-vine (*Smilax pumila* Walt.), sweetgum, and evening trumpet-flower (*Gelsemium sempervirens* (L.) Ait.) were the most abundant seedling, shrub, and vine species surveyed (Table 2). In Turkey Hill, C–L had significantly greater poison ivy abundance relative to CON stands; whereas, SPB had more sweetgum abundance relative to CON stands (Table 2).

Woody plant community

In the overstory and midstory, the first three axes accounted for 17.9% of variation in the data (Table 4), with SPB disturbance explaining the gradient along Axis 1. CON stands are separated from the SPB and C–L stands along axis 1 (Fig. 1A), depicting the loss of pine species from the canopy in each disturbance regime. SPB and C–L stands were associated with primarily hardwood species and showed slight separation in the ordination. SPB stands represent more dominant canopy vegetation not found in C–L stands. The second ordination axis of the CCA was most closely associated with percent slope (Table 4, Fig. 1). Stands with greater slope were depicted to the top along the second axis, with gently sloping stands plotted to the bottom. Species prevalent in mesic areas were associated with steep sloping stands, whereas vegetation common to slope summits were present in stands with gently sloping stands. The overstory and midstory analysis accounted for more percent variance and had higher species–environment correlations of the three analyses (Table 4).

Aspect and elevation accounted for most of the variance in the sapling and shrub (≥ 137 cm height) and seedling, shrub (< 137 cm height), and vine analyses. Each analysis accounted for $\sim 17.0\%$ of variation in the data (Table 4). Stand treatments did not show clear separation in the sapling and shrub (≥ 137 cm height) analysis. South-facing stands at higher elevations are depicted to the left along the first axis, with north-facing slopes and lower elevations plotted to the right in each (Figs. 1B and 1C).

Slope explained the most variance along the second axis in the sapling and shrub (≥ 137 cm height) analysis, but the intraset correlation coefficient was low (Table 4). Similar species assemblages were found across the sloping terrain as the overstory and midstory analysis. Stand age explained the third gradient in the sapling and shrub (≥ 137 cm height) CCA. Treatments did not separate along the third axis, but American beech (*Fagus grandifolia* Ehrh.) and American witchhazel (*Hamamelis virginiana* L.) were common in older stands.

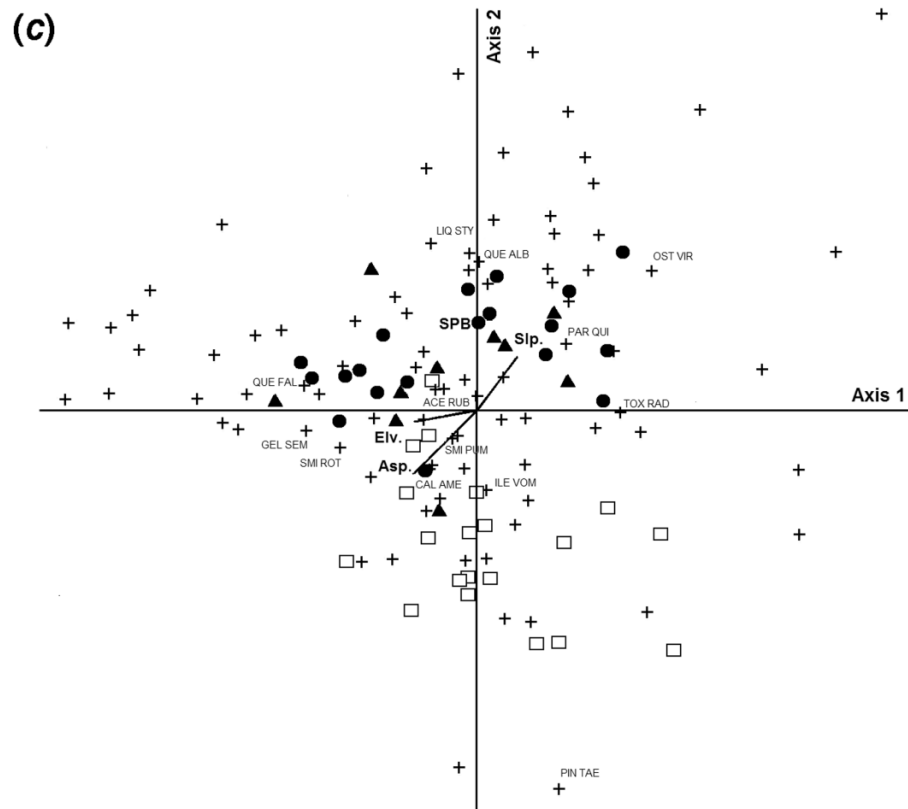
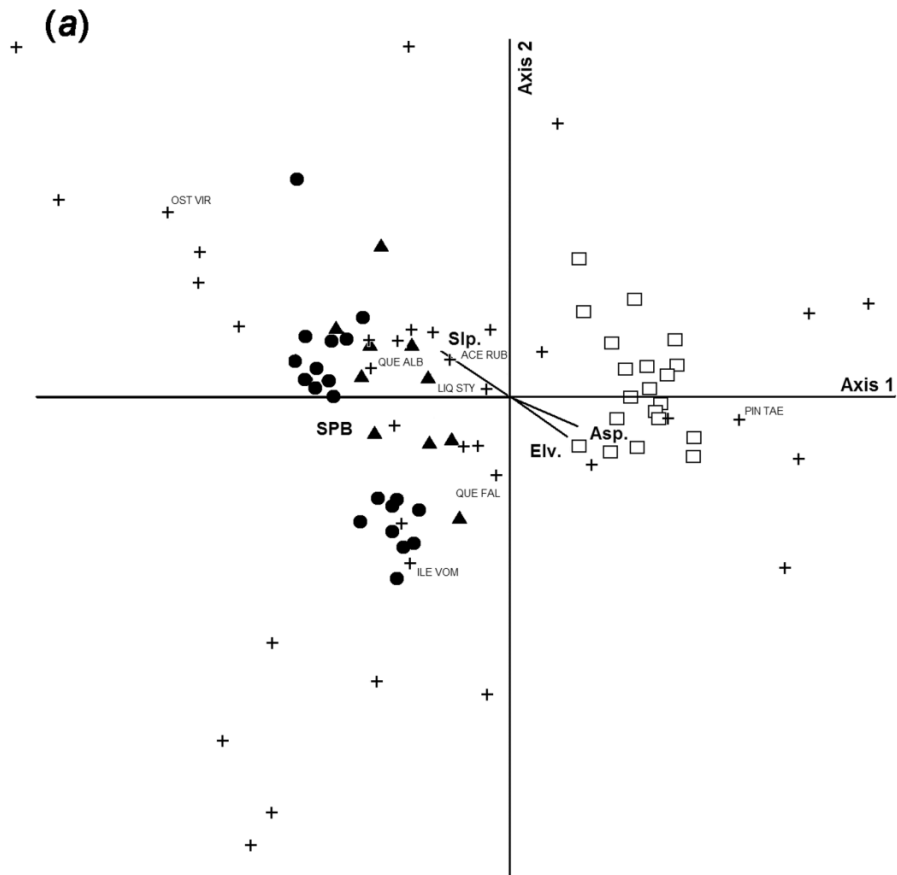
In the seedling, shrub (< 137 cm height), and vine analysis, SPB disturbance explained the second gradient (Table 4). CON stands were plotted to the bottom of axis 2, whereas SPB and C–L stands were plotted to the top (Fig. 1C). Along the second axis, hardwood species including white oak, red maple, sweetgum, and flowering dogwood (*Cornus florida* L.) were prevalent with SPB and C–L disturbances, whereas loblolly pine regeneration was only associated with CON stands (Fig. 1C). The C–L stands separated from CON and SPB stands along axis 3 (Fig. 1D), but the eigenvalue and species–environment correlation were low and may not be influencing species assemblages (Table 4). However, southern dewberry (*Rubus trivialis* L.H. Bailey) and devil's walkingstick (*Aralia spinosa* L.) were prevalent in C–L stands.

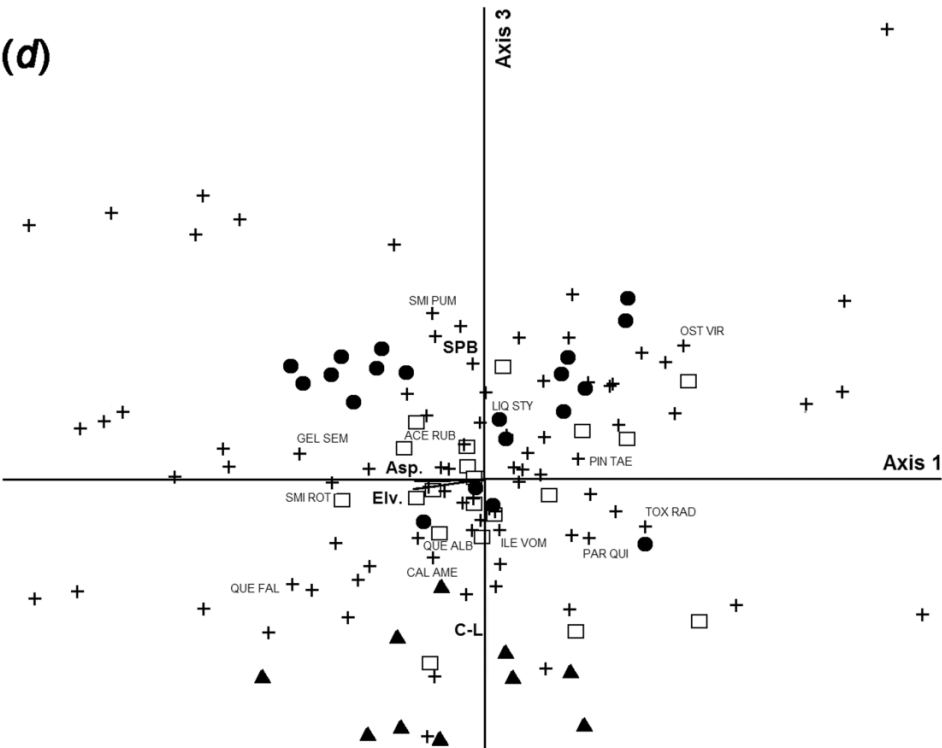
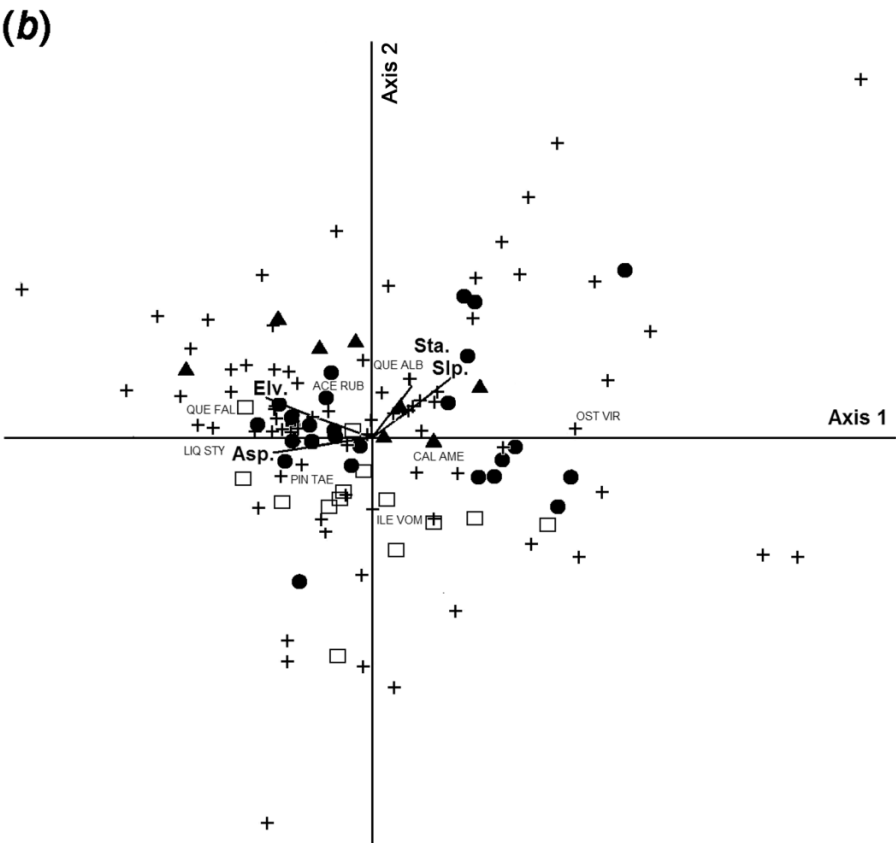
Predicted forest types

Projecting current tree composition 50 years into the future using FVS resulted in five predicted forest types among the three disturbance regimes: mixed upland hardwood (64%), loblolly pine (12%), loblolly pine–hardwood (12%), white oak–red oak–hickory (10%), and red maple–oak (2%). Hardwood dominated stands were predicted significantly more (73%) than pine dominated stands (27%) across the three treatments ($\chi^2_{[1]} = 13.52$, $P = 0.0002$). SPB-disturbed stands were predicted to develop into mixed upland hardwood stands 80% of the time; to maintain their historic loblolly pine composition 5% of the time; or to develop into loblolly pine–hardwood stands (5%), white oak–red oak–hickory (5%), or red maple–oak (5%). The C–L disturbed stands were predicted to develop into mixed upland hardwood (60%), loblolly pine–hardwood (10%), or white oak–red oak–hickory (30%). Lastly, CON stands were predicted to develop into mixed upland hardwood stands (50%), maintain their historic and current loblolly pine composition (25%), or to develop into loblolly pine–hardwood (20%) and white oak–red oak–hickory (5%). Predicted forest types differed significantly between stand treatments ($\chi^2_{[2]} = 8.06$, $P = 0.03$). In SPB and C–L treatments, pine-dominated forest types were predicted to maintain their composition only 10% of the time, whereas 90% of the stands were predicted to shift to hardwood-dominated stands. In CON stands, pine-dominated forest types were predicted to maintain their composition 45% of the time, whereas 55% of the stands were predicted to shift to hardwood-dominated stands.

Discussion

Mortality from SPB and C–L affected nearly 100% of the pine component, decreased overstory and midstory abundance, and reduced richness and diversity in one wilderness.





In both wildernesses, loss of ~67-year-old loblolly pine led to increased hardwood dominance in SPB and C–L stands.

Canopy disturbance increased sapling and shrub (≥ 137 cm height) density, richness, and diversity. In Turkey Hill, C–L enhanced woody vegetation evenness in the overstory and midstory but decreased evenness in the seedlings, shrubs, and vines. Yaupon, American beautyberry, red maple, hophornbeam, and sweetgum dominated the sapling and shrub size class. In Indian Mounds, disturbed stands contained a dense sapling and shrub layer, but vegetation was sparse in the seedling, shrub (< 137 cm height), and vine size class. Greater richness and diversity of seedlings, shrubs, and vines were present at Turkey Hill and in SPB stands.

SPB disturbance accounted for most the variance in the overstory and midstory CCA, whereas elevation and aspect explained the primary gradient among woody vegetation assemblages for the sapling and shrub (≥ 137 cm height) and seedling, shrub (< 137 cm height), and vine size classes. In the seedling, shrub (< 137 cm height), and vine ordination, SPB and C–L disturbances accounted for variation along the second and third axes, respectively. FVS predicts a shift from predisturbance loblolly pine to predominantly mixed upland hardwood communities, and reductions in overstory basal area in both disturbances will still be apparent.

Mortality of dominant canopy pines from SPB and C–L represent different vegetation communities than CON stands in the overstory and midstory because of extensive pine mortality. However, disturbance events did not explain new regeneration present in the understory, demonstrating that these disturbances each influence the plant community in a similar manner and have a relatively minor influence. Stand aspect and elevation, presumably a gradient for moisture, primarily influenced regenerating vegetation. North-facing slopes at lower elevations were associated with hardwood species common to mesic conditions (Burns and Honkala 1990b; Gleason and Cronquist 1991), whereas south-facing slopes at higher elevations were associated with vegetation tolerant to xeric conditions (Burns and Honkala 1990a; Gleason and Cronquist 1991). These results suggest that management efforts should focus on lower slope positions to facilitate pine regeneration by reducing abundant hardwoods. In the Pacific Northwest (US), vegetation composition after a clearcut and slash burning was similarly explained by a moisture gradient, suggesting that the influence of initial species composition and local environment may persist through catastrophic disturbances (Halpern 1988), as seen following mortality caused by SPB and C–L.

Mortality caused by SPB explained the second gradient in the seedling, shrub (< 137 cm height), and vine CCA, which was associated with hardwood species. The second ordination axis represents a shift in succession from pine-dominated, early successional communities present in CON stands to hardwood-dominated, late-successional communities. By only killing pine, SPB selectively killed early succession species, releasing understory hardwoods from competition.

Although C–L was strongly correlated with the third axis (0.72), the eigenvalue and species–environment correlation were low (0.07 and 0.496, respectively). As a result, the interpretation and vegetation associated with the third axis must be used with caution. Woody species tolerant to open-

canopied forests were associated with the C–L gradient (Gleason and Cronquist 1991; USDA NRCS 2005). Woody vegetation associated with these stands may originate from the immediate removal of overstory pines after C–L. Although the woody community following C–L initially differed from those stands disturbed only by SPB, similar forest types dominate each disturbance regime in model projections.

Loblolly pine regeneration was sparse in each of our disturbance regimes. Hardwood competition inhibited pine regeneration following *D. frontalis* disturbance in North Carolina and Arkansas (Balch 1928; Shelton and Cain 1999), similar to our results. Hardwood dominance is obtained from increased growth of existing trees and initiation of new stems, because *D. frontalis* associated disturbances were of sufficient intensity to stimulate understory growth of hardwoods (Harrington et al. 2000). Initial pine densities, ample seed sources, exposed soil, and reduced competition from neighboring trees enhance regeneration and survival of loblolly pine relative to hardwoods after mortality caused by *D. frontalis* (Skeen 1976; Rantis and Johnson 2002; Duncan and Linhoss 2005). Our C–L stands were closer to seed sources than our SPB stands, because C–L was used to protect adjacent pine stands from *D. frontalis*, and are nestled between SPB and undisturbed pine stands. However, dense leaf litter and competition from remnant hardwoods for light, nutrients, and space apparently limited loblolly pine establishment and growth in SPB and C–L stands (Cain and Shelton 2002). Even-aged forests suffering SPB-caused mortality or C–L appear to require additional management or disturbance to hardwoods in the understory, and to the forest floor, to enhance pine composition. Additional fire disturbance has been proposed to maintain pine composition after mortality from *D. frontalis* (Schowalter et al. 1981).

Following SPB and C–L disturbances, predicted loblolly pine basal area suggests a low susceptibility to future *D. frontalis* outbreaks (Hicks 1980). In addition to reducing host material, hardwoods further limit mortality by disrupting *D. frontalis* communication and hindering beetle movement (Schowalter and Turchin 1993). However, the pattern of pine regeneration we observed in the CCA can increase susceptibility to *D. frontalis* because pines are primarily restricted to dense concentrations on dry sites, which increases tree stress. In undisturbed forests, current and predicted densities of loblolly pine constitute a high susceptibility to future *D. frontalis* outbreaks because of dense, overmature, slow-growing hosts (Hicks 1980). Years of management restrictions in wildernesses have promoted high stand densities, increased competition, and ultimately decreased forest health (Duncan and Linhoss 2005).

Disturbances associated with *D. frontalis* accelerated succession to comparable hardwood forest types predicted in much older (~60 years) undisturbed stands. Mechanisms that potentially facilitate disturbance-mediated accelerated succession (Abrams and Scott 1989) include altered overstory competition, changes in microenvironment, and advance regeneration of shade-tolerant species (Chen et al. 2003). Moreover, low pine seed sources, minimal seed establishment, and no subsequent management or disturbance can further limit revegetation of loblolly pine. Natural succes-

sion of woody vegetation in loblolly pine stands following these mortality events appears to be driven primarily by influences from the landscape and initial stand conditions, and not the disturbances themselves.

Forest composition and structure differed approximately 12 years after mortality from SPB and C–L; however, greater differences in composition and structure between the disturbances may be evident immediately following disturbance. Restoration of C–L stands is difficult because of the immediate influx of copious amounts of coarse woody debris to the forest floor, which limits silvicultural options such as prescribed fire. Similar issues are encountered with untreated SPB outbreaks once beetle-killed trees fall to the forest floor, although the influx of woody debris is more gradual. Regardless, both disturbances are predicted to converge to hardwood dominant forests, which compromises softwood timber production but represents greater floral diversity and reduced vulnerability to future SPB outbreaks.

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